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- Northern hare *Lepus timidus timidus* (Tor Lundberg Tuorda, www.kvikkjokk.nu)
- Heath-hare *L. t. sylvaticus* (Kenneth Johansson, www.jagareforbundet.se)
- Red fox *Vulpes vulpes* (www.stylefavor.com)
- Brown hare *Lepus europaeus* (Toni Mikkola, www.cartinafinland.fi)

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Abstract

Scientific and circumstantial evidence of recent decades indicate decreasing population trends in the native mountain hares *Lepus timidus* of Fennoscandia (Finland, Sweden, Norway). It has been suggested that climate warming, habitat degradation, pathogens, predation and interspecific competition are potential candidates to drive this supposed decline. How these ecological mechanisms could function in detail, however, has not been clarified.

In this study I use uncorrected hunting bag data (HBD) densities at the county level to test the relative importance of two hypotheses. First, predation by red foxes *Vulpes vulpes* on mountain hares and congeneric brown hares *Lepus europaeus* will be scrutinized in a historical perspective by means of correlation analysis on the long-term data set for Sweden. Secondly, the potentially competitive influence of brown hares will be studied by conducting a population trend analysis for the whole of Fennoscandia during 1996-2010. Furthermore, the reliability of parts of the HBD used will be evaluated and discussed.

During 1996-2010 mountain hares were declining (OLS linear regression; $b < 0$; $p_b < .1$) in all but one county in Fennoscandia, for which significant population trends could be detected (96% of the sample units). Interregionally, the most negative population trend among mountain hares occurred in region A of southern Sweden (Kruskal-Wallis H test; $p < .000$), de-culminating within a distinct zone around the 58° N latitude. Brown hares were also diminishing in Sweden (region A), but at similar rates as mountain hares did in arctic and boreal Fennoscandia (region B and C). Historically (1960-2010), the majority of the correlated time series sequences of red foxes and either hare species before and after the sarcoptic mange epizootic was not significant. During 1984-1992 negative correlation coefficients between red foxes and mountain hares occur in 59% of all sample units in southern Sweden, whereas only 17% had significant correlation coefficients with brown hares (Spearman rank r_s ; $p < .05$). The complete absence of associations with mountain hares for this region during 2003-2010 is contrasted by 24% positive correlation coefficients with brown hares, which also show to be stronger than before the sarcoptic mange outbreak.

The results support the importance of red foxes and brown hares for mountain hare population dynamics. The current, in some areas alarming, situation for mountain hares in southern Sweden appears to be initiated in most areas by ecological processes during the period 1984-1992. Apparent competition assemblages with red foxes, other predators or the viral disease European Brown Hare Syndrome (EBHS) as deterministic mortality factors might have been influential. During 1996-2010 though the recovery of mountain hares in southern Sweden may rather be prevented by habitat degradation, the Allee effect and possibly hybridization with brown hares. Mountain hare habitat quality in form of winter food and shelter plants as well as landscape stability is expected to be invaluable in coping with diverse threat factors. Based on the population trends detected for mountain hares, Sweden should be partitioned into northern, central and southernmost (below the 59° N latitude) management regions.

Sammanfattning

Forskning såväl som overifierade observationer indikerar minskande populationstrender för den inhemska skogsharen *Lepus timidus* i Fennoskandia (Finland, Sverige, Norge). Det har föreslagits att ett varmare klimat, habitatförstörelse, sjukdomar, predation och konkurrens med andra växtätare kan vara faktorer som driver denna nedåtgående trend. Hur dessa ekologiska mekanismer fungerar i detalj har dock inte klarlagts.

I denna studie analyseras okorrigerade avskjutningsdata på länsnivå, omvandlade till täthetsindex, för att testa två olika hypoteser. Först undersöks med hjälp av en korrelationsanalys i ett historiskt perspektiv hur rödrevens *Vulpes vulpes* predation kan påverka skogshare och den nära besläktade fältharen *Lepus europaeus* i Sverige. Sedan utförs en trendanalys för att påvisa vilken betydelse konkurrensen med fältharen kan ha för skogshare i Fennoskandia. Dessutom bedöms den använda avskjutningsstatistikens förlitlighet.

Mellan åren 1996-2010 minskade skogsharepopulationerna i 95% av alla inkluderade områden, dvs. i samtliga förutom ett län i Fennoskandia, för vilka signifikanta populationstrender kunde fastställas (OLS linjär regression; $b < 0$; $p_b < .1$). Regionen med de lägsta tillväxtvärdena för skogshare var södra Sverige (region A; Kruskal-Wallis H test; $p < .000$). Här är trenderna som mest negativa i en zon omkring den 58° N breddgraden. Samtidigt minskar fältharens avskjutning i Sverige (region A) i liknande takt som skogsharens i arktiska och boreala delar av Fennoskandia (region B och C). Historiskt sett (1960-2010) så har majoriteten av de korrelerade tidsseriesekvenserna mellan rödrev och båda hararterna varit ej-signifikant både innan och efter skabbepidemin på 1980-talet. Negativa korrelationskoefficienter mellan rödrev och skogsharar konstaterades under perioden 1984-1992 i 59% av alla sydsvenka områden, medans bara 17% av korrelationer med fältharen var signifikanta (Spearman rank r_s ; $p < .05$). Den totala frånvaron av associeringar med skogsharar i södra Sverige mellan 2003-2010 motsägs av 24% positiva korrelationskoefficienter med fältharar, som dessutom visar sig vara starkare än före skabbutbrottet.

Resultaten bekräftar den stora betydelsen av både rödrev och fälthare i dynamiken av skogsharepopulationerna. Den aktuella, i vissa områden akuta, situationen för skogsharar i Sydsverige verkar på de flesta håll ha sitt ursprung i ekologiska skeden under tidsperioden 1984-1992. Skenbara konkurrensförhållanden med rödrev, andra predatorer och/eller fältharesjukan (European Brown Hare Syndrome, EBHS) kan vara betydelsefulla deterministiska mortalitetsfaktorer. Mellan 1996-2010 har dock återhämtningen i skogsharepopulationerna i södra Sverige snarare förhindrats av habitatdegradering, Allee effekten och möjligen även hybridisering med fältharar. Kvaliteten av skogsharehabitat i form av vinterfoder- och skyddsväxter samt landskapsstabilitet är uppskattningsvis väsentliga för att kunna motstå diverse hotfaktorer. Med hänsyn till skogshararnas populationstrender borde Sverige indelas i ett nordlig, ett central och ett sydlig (söder om den 59° N breddgraden) förvaltningsområde.

Introduction

Few topics within population ecology are as famous as the co-fluctuating population cycles of snowshoe hares *Lepus americanus* Erxleben 1777 and one of their main predators, Canada lynx *Lynx canadensis* Kerr 1792 ([Brand and Keith 1979](#), [Vik et al. 2008](#), [Tyson et al. 2010](#)). This interlinked periodicity was first documented by Charles Gordon Hewitt ([1921](#)) based on the analysis of trapping bag numbers and shows the amplitudes of the lynx populations to follow those of snowshoe hares quite accurately. Even though predation is believed to play a key role for the hare population to decrease ([Krebs et al. 2002](#)), this phenomenon is still not entirely understood ([Inchausti and Ginzburg 2009](#)). Other hare populations, e.g. palearctic mountain hares *Lepus timidus* Linnaeus 1758 in Europe, exhibit weaker or no cyclicity at all ([Newey 2005](#)). To explain dynamics in such unstable but non-cyclic populations may thus be even more challenging.

Hares (*Lepus*, Lagomorpha) have to face a multitude of predators throughout their worldwide range. The polyphyletic guild consists of i.a. typical carnivores such as felids, canids, or raptors but also of omnivores. Red squirrels *Tamiasciurus hudsonicus* Erxleben 1777 and Arctic ground squirrels *Spermophilus parryii* Richardson 1825 have e.g. been identified to predate on snowshoe hare leverets ([Krebs et al. 2002](#)). Additionally, humans have been hunting hares for flesh and fur throughout their evolutionary history ([Nýltová-Fisáková 2000](#)). Responding to these high predation pressures, hares have been evolving different predator escape strategies. Even so, predation often contributes to mortality rates of up to 90% ([Alves et al. 2008](#)), whereas juveniles are most vulnerable. In order to compensate for such losses, lagomorphs are generally r-selected ([Nowak et al. 1975](#)). Interestingly, Flux ([1981](#)) found that the number of offspring per female and breeding season within the genus *Lepus* appears to be approximately constant, while the number of litters over a year decreases with increasing latitude.

When taking all threat categories into account (CR, EN, VU and NT), *Lepus* has today most threatened species among eight concerned lagomorph genera ([IUCN 2013](#)). Moreover, hare hunting bag records across major parts of Europe signify decreasing population trends for last decades ([Smith et al. 2005](#)). This tendency contrasts the finding of Geiser and Turbill ([2009](#)) that smaller-sized mammals commonly seem to be most resistant to extinction threats but might substantiate that “sleep-or-hide” mammals were disproportionally less threatened with extinction compared to non-sheltered mammalian species ([Liow et al. 2009](#)). To enhance alertness among researchers and wildlife managers alike, Ceballos and Ehrlich ([2002](#)) emphasize the importance of considering decreasing populations at an early stage because these reasonably form the pillars of any species that may become threatened in the future.

When explaining ecological mechanisms that lead to population declines, the miscellany of environmental and human-induced processes often aggravates attempts to discriminate causative factors. However, in the ongoing sixth extinction crisis ([Barnosky et al. 2011](#)) either a combination or single element of what has become to be known as the “evil quartet” ([Western and Pearl 1989](#)) is likely to be involved. These four factor groups are habitat destruction, extinction chains, overkill, and competition with or predation by neobiota. Interestingly, more unobvious ecological processes, such as population genetics, adhered initially less attention. Various examples and consequences of interbreeding, intergradation, and hybridization ([Arnold et al. 1991](#)) following establishments of non-native species are reviewed for multiple taxa from different ecosystems ([Hubbs 1955](#), [Rhymer and Simberloff 1996](#), [Simberloff 1996](#)). Within the genus *Lepus*, gene introgression across the

species barrier is frequently occurring in the wild ([Thulin et al. 1997](#), [Melo-Ferreira et al. 2005](#), [Fredsted et al. 2006](#), [Thulin et al. 2006a](#)) and often leading to fertile offspring.

In disparity to the “evil quartet”, changes in climate have a rather extensive efficacy. Most scenarios concerning the current climate warming period project increasing annual mean temperatures as well as distorted precipitation events to be particularly pronounced in arctic and sub-arctic regions ([Brodersen 2005](#)). Stocker et al. ([2013](#)) postulate, that current snow cover line and -period as well as the snow depths and -quality will very likely further decrease or shrink northwards, respectively. Consequently, species with seasonally dimorphic pelage such as arctic or boreal hares, other mammals (e.g. *Alopex lagopus*, *Mustela erminea*, *M. nivalis nivalis*, *Dicrostonyx groenlandicus*) and birds (*Lagopus lagopus*, *L. muta*) will face the threat of more days with a mismatch between their winter coat coloration and the surrounding environment. Thus, Mills et al. ([2013](#)) suggest that predation mortality in these species caused by visual predators will probably increase in the near future.

In Fennoscandia two different hare species occur; the native mountain hare *Lepus timidus* and the only recently established brown hare *Lepus europaeus* Pallas 1778. With the retreat of the Weichselian glaciers, mountain hares began to recolonize the Scandinavian Peninsula. The earliest fossil records from the southern tip of Sweden ([Lepiksaar 1986](#)) indicate that this range expansion started more than 12,000 YBP (Years Before Present) across a land bridge connecting Scandinavia with the European mainland ([Björck 1995](#)). Bergengren ([1969](#)) suggests a bi-directional recolonization of Scandinavia from the south and northeast via Karelia, finally creating an intraspecific hybrid contact zone between the 59° N and 61° N latitudes. Similar biogeographic convergence of mammals has been discovered in Scandinavia e.g. for Eurasian brown bears *Ursus arctos arctos* L. 1758 ([Taberlet et al. 1995](#)) and bank voles *Myodes glareolus* Schreber 1780 ([Jaarola et al. 1999](#)). Bergengren ([1969](#)) argues that the nominate subspecies northern hares *Lepus timidus timidus* L. 1758 with a woollier almost pure white winter coat dominates all over Fennoscandia except within and south to the hybrid contact zone in Sweden. Here, heath-hares *L. t. sylvaticus* Nilsson 1831 represent the species successively being better adapted to milder winters by molting to a more blue-grayish, black sprinkled pelt ([Angerbjörn and Flux 1995](#)). According to Middendorff in Bergengren ([1969](#)) this subspecies also appears, although less abundant, alongside the Swedish coastline of the Bothnian Bay. Angerbjörn and Flux ([1995](#)) describe the genetic differentiation between these two subspecies as a result of a dominant (pure white) recessive (blue-grayish) allele pair coding for the winter pelage color. Furthermore, differences in haplotype mtDNA distribution are found across Scandinavia but with a large overlap and high degree of relatedness between northern hares from Fennoscandia and Russia ([Thulin et al. 2003](#)).

The colonization history of brown hares in Fennoscandia starts in the second half of the 19th century. This temperate hemerophilic species dispersed naturally from the south into Finland across the Russian border as late as approximately 150 YBP ([Schröder et al. 1987](#)). On the other side of the Baltic Sea, the establishment of brown hare populations on the Scandinavian mainland was initiated by iterative introductions beginning in the southwest of Skåne County, cf. Appendix p. I ([Lönnberg 1908](#)). Coinciding with these first brown hare appearances the range of heath-hares began to shrink north-east-wards until its local quasi-extinction for this county was confirmed at the brink of the 21st century ([Thulin and Tegelström 2002](#)). Further self-reliant dispersal and continued releases of brown hares also north of Skåne County ([Thulin et al. 2006b](#)) rapidly formed the current Scandinavian range with a fairly stable northern border around the 60° N latitude. The distribution grossly

overlaps with the entire former allopatric range of heath-hares and the intraspecific mountain hare hybrid zone ([Bergengren 1969](#)). Introduction attempts north to the 61° N latitude failed ([Thulin 2003](#)). Interestingly, brown hares did until today not disperse further into Norway than the south of Østfold County ([Mitchell-Jones et al. 1999](#)). Recently, however, Jansson and Pehrson ([2007](#)) reported for Sweden that brown hares have established north to their former border zone and even at higher altitudes. Meanwhile, brown hares in Finland spread already along the coast of the Bothnian Bay much farther into the taiga ([Mitchell-Jones et al. 1999](#)).

Circumstantial evidence as well as published literature on this topic indicate the decline in mountain hares of Scandinavia at the local scale from a historical perspective ([Lönnberg 1905](#), [Lind 1963](#)) and nation-wide starting during 1980's ([Thulin 2003](#), [Jansson and Pehrson 2007](#)). Changes in climate and phyto-geographic habitat structures have been considered to negatively affect both occurring hare species. The clearing of bushes and thickets to ameliorate the growth of preferred cultivated plants principally equals the reduction of valuable hide and retreat areas and winter food supply ([Krebs et al. 2002](#)). Further on, Fennoscandia is inhabited by large birds of prey (e.g. *Aquila chrysaetos*, *Accipiter gentilis*, *Bubo bubo*, and *Buteo buteo*), medium-sized mustelids (e.g. *Martes martes*, *Neovison vison*), recently recovering large carnivores (*Lynx lynx*, *Gulo gulo*, *Canis lupus*) and even opportunistic omnivores (*Ursus arctos*, *Meles meles* or *Sus scrofa* and *Nyctereutes procyonoides*). All of these will at least occasionally predate on hares. However, even red foxes *Vulpes vulpes* L. 1758 do usually not focus on hares as an exclusive food resource. Nevertheless, this versatile and ubiquitous predator species has the capacity to locally exterminate ([Angerbjörn 1989](#)) and regionally limit total population sizes ([Carlsson et al. 2010](#)). Moreover, the state of interactions between mountain and brown hares is not yet fully understood. Thulin ([2003](#)) balances potential factors causing the apparent decline of mountain hares and contemplates the possibility that mountain hares are competitively excluded by brown hares. Even though a slight habitat overlap exists, the ecological niches are differentiated. Brown hares can be classified as year-round grazers of steppes and agricultural lands, whereas mountain hares of Fennoscandia rather show the tendency to selectively browse mires or forested as well as mountainous regions. Recently, however, this habitat segregation seems to lessen even further due to brown hare population establishments in former typical mountain hare habitats ([Jansson and Pehrson 2007](#)). From a genetic point of view, the recruitment of fertile hybrids holds true for the species pair *europaeus/timidus* ([Gustavsson and Sundt 1965](#)) and about 10% of the brown hares in Sweden bear mountain hare mtDNA ([Thulin and Tegelström 2002](#)). Although crossbred individuals have been early reported from Sweden ([Lönnberg 1908](#)) and confirmed by means of molecular techniques ([Thulin et al. 1997](#)), the observations of this phenomenon in Finland have until today not been substantiated by rigorous genetic analysis ([Jaakko Pohjoismäki 2013](#), pers. comm.). In contrary, Schröder et al. ([1987](#)) conclude that hybridization did not occur (n=42) in the wild within Finland.

For hare populations in Sweden it has been shown that mtDNA introgression occurs most often unidirectional from mountain towards brown hares ([Thulin et al. 1997](#), [Thulin and Tegelström 2002](#)). This indicates that mating between brown hare males and mountain hare females, hybrid survival and successful backcrossing of hybrids into brown hare populations would lead to functional litter transmission from mountain to brown hare populations. Despite morphometric inferiority of the arctic-boreal mountain hares, it remains to be explained to which extend intraspecific competition like aggressive dominance behavior for food resources and mate guarding, common among brown hares, are projected upon the intrageneric level. In addition, the consequences of intergradation

between heath-hares and northern hares as a result of the latter subspecies being translocated far south to the intraspecific hybrid zone have not been addressed scientifically.

In summary, there seems to be consensus ([Thulin 2003](#), [Jansson and Pehrson 2007](#), [Kauhala and Helle 2007](#), [Pedersen and Pedersen 2012](#)) that climate warming, habitat degradation, parasites and diseases, interspecific competition and predation have the capacity to drive the apparent decline of mountain hare populations in Fennoscandia. How these ecological mechanisms function in detail has not yet been clarified. Similarly, the established knowledge on hybridization and interspecific gene flow has not been integrated into a larger ecological framework. In spite of these shortcomings, no extensive approaches have been undertaken to unveil the mechanisms behind the decline in mountain hares. Besides, this highly esteemed game species and vivid symbol of the north is nationally monitored only in Finland.

In this study I test the relative importance of red fox predation on both occurring hare species and intrageneric hare interaction by analyzing hunting bag data of mountain hares, brown hares and red foxes from Fennoscandia (Finland, Sweden and Norway). Moreover, I describe spatial differences and similarities with respect to hare biogeographic distribution regions (cf. Fig. 1). Especially, the data gathered in Sweden is unique by covering more than 50 consecutive hunting seasons and has earlier been investigated concerning other ecological questions ([Carlsson et al. 2010](#)). Furthermore, I will partially evaluate the reliability of the data used by creating catch-per-unit-effort (*CPUE*) time series for the hare species in Sweden and compare the Finnish data set to population density indices based on wildlife triangle inventory results. In line with the described reasonings from the published literature, I formulate two working hypotheses explaining the perceived decline in mountain hares.

Hyperpredation hypothesis (H_α)

Considering the vulnerability of hare populations to predation in general, and the documented impact of red foxes on mountain hares in Fennoscandia in particular, I put forward that abiotic habitat alterations as well as biotic ecosystem processes led to enhanced overall predation pressure and thus causing the downturn in mountain hare populations.

Competitive exclusion hypothesis (H_β)

Any direct negative impact on mountain hares that can be linked to increased fitness in brown hares should have stronger numerical consequences in parapatric than in allopatric mountain hare populations. Accordingly, I hypothesize that parapatric brown hares have stable or increasing population trends, whereas mountain hare populations decrease more notably than in allopatry and in converse relation to population dynamics in brown hares.

In order to test these hypotheses on hunting bag data at two spatial scales in Fennoscandia, this study aims at (1) describing the influence of the supposedly most important predator on both hare species (H_α), (2) scrutinize population trends whether patterns can be found, which promote the impact of competitive interactions between mountain and brown hares (H_β) and finally (3) elucidate the reliability of parts of the hunting bag time series used.

Methods

Study area

The study includes most of the Fennoscandian Peninsula located in northern Europe between the 55° and 70° N latitudes and around the 20° E longitude, see Fig. 1. The three countries Norway, Sweden and Finland are represented by hunting bag time series of 55 administrative subunits except the island of Åland. A total of four prevalent terrestrial biomes are characterized by managed boreal forests, dominated by Scots pine *Pinus sylvestris* L. 1758 and Norway spruce *Picea abies* L. 1758, the Scandinavian mountain chain, inland

freshwater bodies and, finally, the denser populated and more agriculturally used area of southern Scandinavia. The Baltic Sea along with the continental influence from European Russia and the Gulf Stream in the east Atlantic are central to the overall cold and dry climate in the area.

Numerous large mammals, which have gone extinct in remaining Europe, are present or recovering.

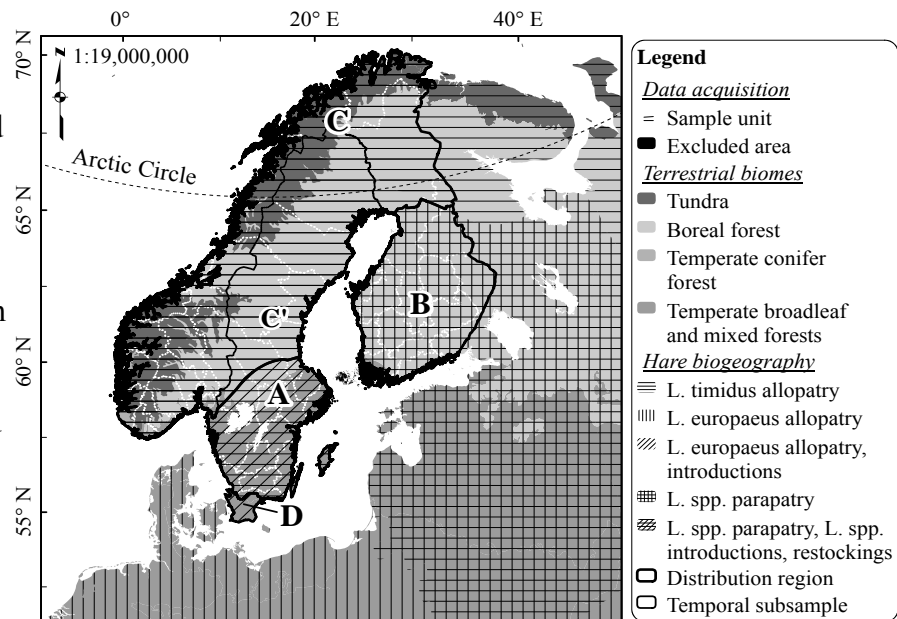


Fig. 1: Study area within Fennoscandia (Finland, Sweden and Norway) divided into four major distribution regions based on hare biogeography. A sample unit corresponds to one county or hunting district (State: 1996 onwards; Projected coordinate system: SWEREF 99 TM; Graticule: Decimal degrees; References see main text).

Data

Hunting bag records of the studied species for the counties of Sweden and Norway were acquired from The Swedish Association for Hunting and Wildlife Management (www.viltdata.se) and Statistics Norway (www.ssb.no), respectively. For the county-like hunting districts of Finland the hunting bag time series as well as wildlife triangle indices were extracted from online databases (www.riistaweb.riista.fi and www.rktl.fi) maintained by the Finnish Game and Fishery Institute. In all countries hunting bags are voluntarily reported and consist of the number of harvested individuals during one hunting season (from now on called census season). For both hare species this endures with regional differences from early September until late February, whereas red foxes can be shot practically from mid July (Norway) or the beginning of August (Finland, Sweden) until the start of their reproductive season during March-April. These slight differences were not accounted for in the data analysis. The hunting bag time series cover different periods of time. For Sweden the data collection stretches from census season 1960/61 (from now on 1960) until 2010. Records from Finland and Norway depict hunting bags from 1996 to 2010. Missing data values were calculated as the mean of adjacent census seasons. For Finland, the

utilized wildlife triangle data originates from two spatially separated census regimes, both applying the same method described by Lindén et al. (1996). The number of individual tracks are counted and related to a measure of effort, i.e. the route length and day (number of tracks per 10km per 24h). The “hare dog” data on the national scale for Sweden stem from the Swedish Kennel Club (www.skk.se) and resemble the number of pedigreed pups per year of preselected dog breeds typically used in hare hunting. Following the advices of Helena Nyberg (2013, pers. comm.), I estimated the fraction of preselected breeds (Finnish hound, drever etc.), that presumably are used in hunting purposes. The annual data was averaged between two successive years to approximately match the period of a census season lasting from autumn until mid to late winter.

Where county boundaries were changed, hunting bag records for Sweden were joined to equal current county divisions. In the comparative analyses described below, total hunting bag numbers were related to the sample unit’s land area. To mirror the parapatric and allopatric hare distribution regions, certain time series were divided among or completely assigned to parts of a concerned sample unit (i.e. Värmland, Dalarna, Gävleborg, Skåne County and Oulu hunting district). The areal proportions needed for this work, were received by geospatial analysis of the hare species distribution data (Mitchell-Jones et al. 1999, IUCN 2013) as well as the location of administrative boundaries and inland water bodies (Bauer 2010). Finally, the hunting bag data were split into four major distribution regions, see Fig. 1; two parapatric regions A and B (southern Sweden excluding most of Skåne County for the time period 1996-2010 and central-southern Finland), mountain hare allopatry C covering Norway, the northern part of Sweden (C’) and northernmost Finland as well as brown hare allopatry D. Recent sporadic appearance of brown hares in the hunting bag records from region C was neglected and equally considered to be allopatric mountain hare region as Østfold County. In contrast, Kainuu was included into region B.

Statistics

For the statistical analyses five auxiliary assumptions were made: (1) the hunting bag data (HBD) densities of the harvested species describe the dynamics of real population densities parallel; (2) HBD of different origin are comparable because acquisition, quality and reliability do not vary across or within the countries of Fennoscandia nor through time; (3) Hare and fox catchability are not density-, ecology- nor weather-dependent, thus hunting success was proportional to hunting effort; (4) in counties which are divided by biogeographic boundaries the species dispersion and hunting pressure did not follow a gradient perpendicular to these boundaries; (5) excluded HBD would not notably influence the results.

The hyperpredation hypothesis (H_a) was then tested in a historical perspective on the land area related hunting bag records from 21 counties of Sweden (A and C’; N=24). To retrieve differing regimes within the two red fox time series, the sequential t-test analysis of regime shifts STARS (Rodionov 2004) was utilized on the regionally summarized and ln-transformed data subsets. This algorithm holds the advantage of objectively identifying regime shifts even at the end of the time series and points out the statistically significant difference *diff* between the mean values of two adjacent sequences by applying ordinary Student’s t-tests:

$$diff = t\sqrt{2\sigma_l^2 / l}, \quad (I)$$

where l is the cut-off length of the regimes, σ_l^2 the average variance and t the t-distribution value at $2l-2$ df. The specifications were set to a cut-off length $l=10$ years and a Huber weight equal to 1. For the derived regime sequences Spearman rank correlation coefficients

r_s were computed on the county level between each hare species' time series sequence and that of red foxes. The null hypothesis was tested if these time series sequences are not correlated ($H_0: r_s=0$). Since prior conducted cross-correlation analysis did not indicate delayed patterns, hunting bag records were compared per census season. However, to describe the direct predation impact more specifically as a driving factor of hare population decline the red fox population density index was also related to the finite rate of increase $\lambda_{t \rightarrow t+1}$ in the hare populations within the direct following reproduction period:

$$\lambda_{t \rightarrow t+1} = DI_{t+1} / DI_t, \quad (II)$$

with DI_t and DI_{t+1} being the hare density indices of two consecutive census seasons.

To test the competitive exclusion hypothesis (H_β) a spatial comparison of the land area related HBD from 1996 to 2010 was performed at both the sample unit and interregional scale. All hunting bag density indices for 15 consecutive census seasons (N=60 sample units) were regressed on time, using ordinary least square (OLS) linear regression. The regression coefficients b_{ts} of significantly or with a tendency ($\alpha=.1$) fitted lines were extracted to build derived samples of hare population trends in the different distribution regions. Here, stable population dynamics were also included, whenever the null hypothesis ($H_0: b_{ts}=0$) was accepted ($p>.9$). The equations given below in the text represent the regression lines and follow the general linear formula:

$$y = a + xb, \quad (III)$$

where y (alternatively: x_2) is the natural logarithm of the land area related HBD [$\ln(\text{HBD}/10\text{km}^2)$] per species and sample unit, x (x_1) the time steps of census seasons, a the intercept with the y-axis, and b the estimated slope of the regression line. A nonparametric equivalent of the Levene's test was employed to judge whether the derived samples fulfill the assumption of distribution similarity. Due to non-normality of derived samples the nonparametric Kruskal-Wallis test statistic H was calculated (Siegel 1956) to examine the null hypothesis of no significant differences between the group mean ranks x_{rank} for the species population trends of the different regions ($H_0: \Delta x_{rank}=0$). In case a statistically significant divergence was detected, the identification of the differing group mean rank pairs was accomplished by applying the post-hoc Tukey HSD test according to:

$$HSD = \frac{q_{(\alpha, k, \infty)}}{\sqrt{2}} \sqrt{\frac{N(N+1)}{6n}}, \quad (IV)$$

with q being the value obtained from the q -table, k equal to the number of samples, α as significance level, ∞ being the degrees of freedom for the error value in the χ^2 -distribution table, N equal to the total sample size and n as the size of the smallest sample in the analysis. Additionally, it was explored, whether or not the species population trends b_{ts} of the time series showed a spatial pattern by using scatterplots along Y -ordinate values describing the distance from the polygon centroid of a sample unit to the Equator.

The HBD reliability was put to test in two different ways. First, the pooled hare species HBD from Sweden of the time period 1976-2010 were divided by the number of pedigreed "hare dog" pups. Thereby, two catch-per-unit-effort (CPUE) indices were created. Secondly, I regressed the time series of wildlife triangle indices per species on the HBD density index from Finnish hunting districts (1996-2010) by using OLS linear regression.

If not specifically outlined otherwise, the statistical analyses were conducted at the significance level of $\alpha=.05$. All methods described were performed in IBM®SPSS Statistics 20 or Microsoft®Excel 2003, respectively.

Results

Hyperpredation

The literature review concerning the importance of hares as prey species yielded insights gathered in Table 1. The majority of the studies employed the traditional frequency of occurrence (FO) method and identified remains of prey specimens by categorizing morphological traits. Investigations conducted for para- or sympatric areas did not account for differences between mountain and brown hares, but instead pooled these two species (*Lepus spp.*). Red foxes, but also northern goshawks *Accipiter gentilis* and lynxes *Lynx lynx* appear to be those wild predators, which temporarily focus on hares as primary prey. The tabulated information does, however, not reveal which predation pressures could drive local hare populations and, moreover, cause severe declines at the regional scale.

Table 1: Proportion of hares *Lepus spp.* in the diet of different predator species from Fennoscandia and remaining Europe.

Predator	<i>Lepus sp.</i>	Proportion	%	Period	Data	Reference
<i>V. vulpes</i>	<i>timidus</i>	<1–20	FO	autumn	scat	Lindström (1982)
<i>V. vulpes</i>	<i>timidus</i>	38–94	BM	w,spring	scat	Angerbjörn (1989)
<i>V. vulpes</i>	<i>L. spp.</i>	57–59	FO	summer	scat	Kauhala et al. (1998)
<i>M. martes</i>	<i>L. spp.</i>	8.15	BM	winter	scat	Helldin (1999)
<i>L. lynx</i>	<i>L. spp.</i>	79.5	FO	winter	stomach	Pulliainen (1981)
<i>L. lynx</i>	<i>timidus</i>	15.7–22.9	FO	winter,s	trc,scat	Odden et al. (2006)
<i>G. gulo</i>	<i>timidus</i>	12.7–15.6	FO	denning	scat	Koskela et al. (2013)
<i>C. lupus</i>	<i>L. spp.</i>	1.9	FO	year	scat	Müller (2006)
<i>A. gentilis</i>	<i>timidus</i>	69.6	BM	winter	tracking	Tornberg and Colpaert (2001)
<i>B. buteo</i>	<i>L. spp.</i>	17.8	BM	breeding	pellet	Reif et al. (2001)
<i>A. chrysaetos</i>	<i>timidus</i>	5.6	FO	breeding	pellet	Nyström et al. (2006)
Fennoscandia (Finland, Sweden and Norway)						
<i>V. vulpes</i>	<i>europaeus</i>	3.7–41.7	VO	winter	stomach	Panek (2013)
<i>V. vulpes</i>	<i>L. spp.</i>	1.3–5.1	FO	year	scat	Sidorovich et al. (2006)
<i>C. lupus</i>	<i>europaeus</i>	5.2	FO	year	scat	Ansorge et al. (2006)
<i>B. bubo</i>	<i>europaeus</i>	8.5	BM	breeding	trc,pellet	Sándor and Ionescu (2009)
Europe (except Fennoscandia)						
Abbreviations: % - percentage; FO - frequency of occurrence, BM - bio mass consumed, VO - volume; w - winter, s - summer, year - all year round; trc - tracking and non-consumed prey remains.						

Regime shifts in the red fox population dynamics of Sweden were determined at the regional level for the period 1960–2010. The sums of sample unit HBD densities measured in number of individuals harvested per census season and sample area (Σ [HBD/10 km²/sample unit]) were tracked over time. The application of the STARS technique on the summed red fox time series yielded different results (cf. Appendix p. II) for the two hare distribution regions A (n=17 counties) and C' (n=7). While three regime sequences were detected for northern Sweden, four were found for the parapatric region A. However, the third regime shift in C' happening during census season 2009 introduces the fourth sequence also in this subregion. In both cases, the first sequence describes fairly stable to fluctuating population dynamics. Despite the rectifying influence of density calculus and ln-transformation the red fox and mountain hare HBD in northern Sweden appear to have a weak cyclicity with a period length of 3–4 years before 1980. The second sequence for southern Sweden depicts a sharp decline and initial recovery of the red fox population density index after the negative peak in census season 1989. For the northern region a similar, although less distinct pattern is perceivable. The decline begins some years earlier

than in region A and there is no apparent negative peak. For southern Sweden the third and fourth regime sequences show a stepwise augmentation in population densities, whilst the former population densities of the first regime sequence are reached as late as 2002. For visual comparison the results of the regime shift detection procedure for all three hare time series are plotted alongside those for red foxes.

Correlation coefficients allow to a certain degree to interpret effects on prey populations. The outcome of the correlation analyses between population density indices for red foxes and the hare species from the same census season is visualized in Fig. 2. Here, all Spearman rank correlation coefficients r_s for which the null hypothesis H_0 was rejected are included (29% of all possible correlations for region A and C' together). A general pattern apparent for both northern and southern Sweden is the dominance of negative associations during the central regime sequences. However, in the southern region the majority of correlations between brown hare and red fox density indices is not significant for the period 1984-1992. During approximately the same time period in 58% and 57% of the sample units from region A and C', negative correlations ($p < .05$) between mountain hare and red fox indices dominate. In contrary, before and after the perceived red fox population downturn and partial recovery during the late 1980's, positive associations outweigh the number of negative ones, which only appear during the first regime sequence in southern Sweden. In the same region no correlates with mountain hares and only few positive (23.5% of 17 sample units) with brown hare indices were found for the period between census season 2003 and 2010.

The additional correlation analysis between red fox indices as original HBD of a given census season and the calculated estimates of the finite rate of increase $\lambda_{t \rightarrow t+1}$ for each hare species towards the following census season yielded only few significant associations, cf. Appendix p. III (Spearman rank correlation: $-.85 < r_s < .756$; $P < .05$ with mountain hares; $-.763 < r_s < .933$; $P < .036$ with brown hares, H_0 was rejected in 7% and 15% of country-wide 158 possible outcomes).

The population trend analysis described below revealed certain patterns for mountain hares and red foxes for Sweden. The regression coefficients b_{ts} are plotted against the latitudinal measure of the Y-ordinate (cf. Fig. 3). The eye-fitted line for mountain hares points out a zone approximately between $\psi = 64 \cdot 10^5$ m and $65 \cdot 10^5$ m (Y-ordinates, geodetic reference

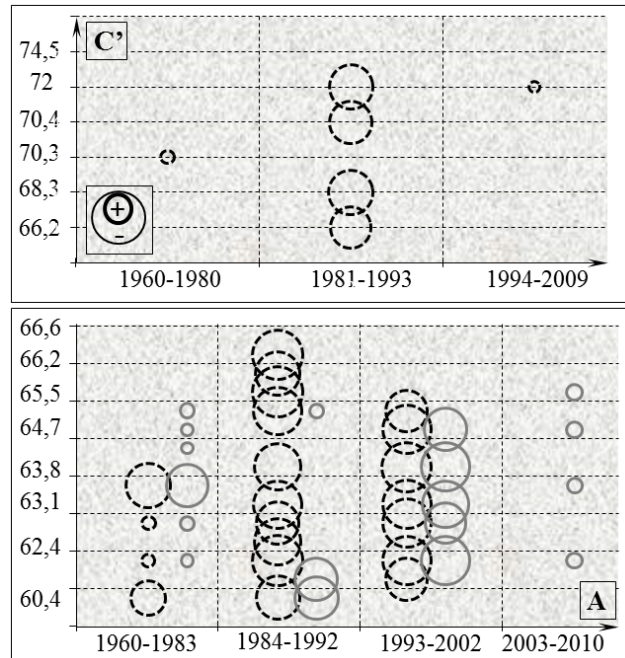


Fig. 2: Bubble chart depicting relative strength and type of significant correlation coefficients r_s for the species pairs red fox and either hare species (broken circles: mountain hare; solid: brown hare). The superimposed bold reference circle separates the largest positive from the smallest negative r_s . One circle represents one sample unit from distribution region A or C' at the latitudinal location (y-axis in 10^5 meters, SWEREF 99) of its polygon centroid during one red fox regime sequence on the x-axis (data table see Appendix p. III).

system SWEREF 99) equal to an area around the 58° N latitude, in which the negative population growth had been highest. In contrary, red foxes have positive population growth in most of the sample units. However, within the latitude range between about 56.8° N and 61.3° N these trends appear to be halted to regression coefficients with $.019 < b_{ts} < .038$.

Competitive exclusion

To investigate potential hare interactions, the data set was shrunk to the more recent period between the 1996 and 2010 but spatially extended to incorporate time series from Finland and Norway. Due to diffuse frequency distributions in the time series data the median is shown as a summarizing statistic in form of histogram maps, see Fig. 4. Interestingly, brown hares appear in the hunting bag records of all sample units except for Norwegian counties. However, in distribution region C they occur at such low densities, that this species was treated as if absent, equally as mountain hares appear to be on the Island of Gotland in the Baltic Sea and in most of Skåne County (Sweden, region A and D, respectively). The latter, in contrary, yields by far the highest numbers of brown hares almost reaching 30 individuals per 10 km² on average. In central-eastern Finland, conversely, more than 30 mountain hares were shot on average per 10 km² within the hunting district of Pohjois-Savo. Between these extreme values there are gradients perceivable in the median hunting bag records of both hare species within region A and B. While average mountain hare HBD density increase, those of brown hares decrease along an imaginary line from Gotland towards the Scandinavian Mountains and from Åland archipelago with north-eastern orientation. During the 15-year data period, similar HBD densities of red foxes and brown hares were detected for Finland and Sweden, whereas twice as much mountain hares were harvested in Norway compared to Sweden. In Finland, unexpected 9.3 times more mountain hares were bagged on average than in Scandinavia.

Every sample unit of the distribution regions A, B, C and D was included (N=60). Since no dependence between the bivariate data is expected for logical reasons, the output of adjusted R² values was overlooked. Regression coefficients b_{ts} for mountain hares were in 96% of the cases (n=59) accepted as statistically significant trend estimates. In all but one sample unit, Finnmark County ($y = -.907 + .032x$; $p_b = .061$), the hunting bag time series of mountain hares show a decreasing trend of differing degree. The sharpest decline was discovered for Stockholm County ($y = .313 - .212x$; $p_b < .000$). Least declining trends in mountain hare populations were revealed for the sample units of Jämtland, Etelä-Häme, Norrbotten and Troms. For brown hares, significant regression lines were detected in 61% of the sample units inhabiting this species, n=33. As a matter of fact, 36% of the insignificant lines were supposed to represent sample units from region B. The slopes of the three significant regression lines for brown hares from this region show one weakly declining (Rannikko-Pohjanmaa) and two positive population trend estimates (Etelä-Häme,

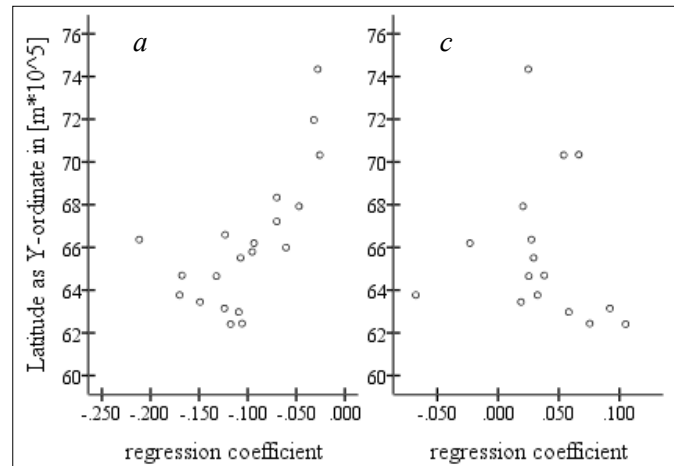


Fig. 3: Accepted regression coefficients b_{ts} for Swedish counties (N=21) as mountain hare (a) and red fox (c) population trend estimates between 1996 and 2010. These are plotted against the latitudinal location of the county centroid measured as Y-ordinate in 10⁵ meters (SWEREF 99).

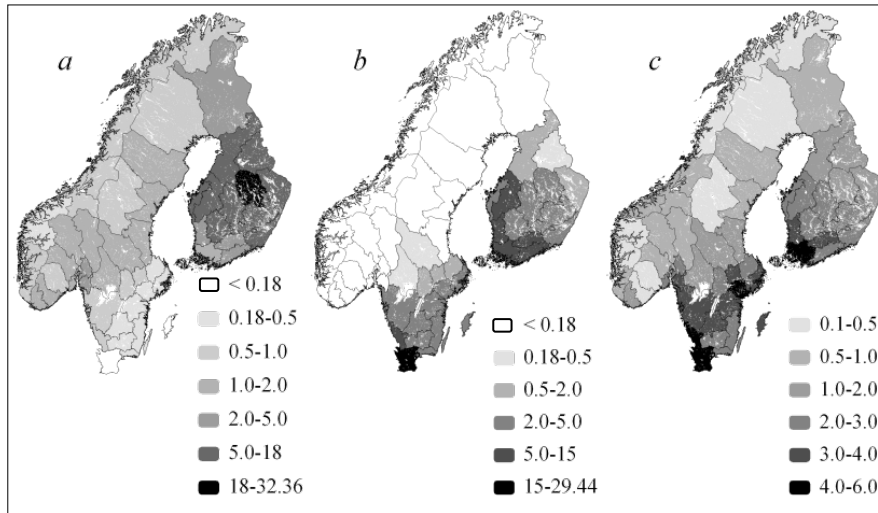


Fig. 4: Histogram maps for mountain hares (a), brown hares (b) and red foxes (c) showing county-wise hunting bag densities as the median number of harvested individuals per 10 km² and sample unit for the time period 1996 to 2010. Note that bin sizes have been set species for each species and the data acquisition is based on nationally differing census regimes (References see main text).

Kaakkoi-Suomi). In the latter sample unit the highest increase in all hare populations was found ($y = .878 + .047x$; $p_b = .001$) for brown hares, while the mountain hare population trend was estimated to be moderate ($y = 2.293 - .046x$; $p_b = .004$). Furthermore, these three sample units seem to be located in an arc-shaped manner adjacent to the area, in which highest numbers of brown hares (5-15 individuals per 10 km², cf. Fig. 4) were harvested on average per census season. The only significantly stable population trend in brown hares from region A were found in the parapatric part of Värmland ($y = -1.156 + .003x$; $p_b = .908$). As for mountain hares the steepest negative slope in brown hare population trends was discovered for Stockholm County ($y = 1.517 - .099x$; $p_b < .000$). In general, mountain hares of region C appear to decline at higher rates in south-western parts (i.e. south of Norway) compared with those towards the north-east. In northern Finland this pattern turns, again, into conditions prevalent in southern Norway. South to these hunting districts a threshold latitude zone between $\psi = 70 \cdot 10^5$ m and $\psi = 71 \cdot 10^5$ m demarcates a break in the severity of the estimated mountain hare population declines. Within this zone four sample units show a distinct west-east difference. While Pohjois-Savo ($y = 3.952 - .056x$; $p_b < .000$) with overall highest hunting bag records for mountain hares at the starting census season 1996 (>90,000 harvested individuals), and Pohjois-Karjala represent a moderate decline, hunting districts closer to the Baltic Sea (Pohjanmaa and Rannikko-Pohjanmaa) have more profound negative population trends. However, with these slope estimates they would still fit into the group of least declining mountain hare populations of distribution region A (see Fig. 3). Remarkably, the population declines first increase in severity with rising latitude, but take a distinct turn to ease out the farther to the north the sample units are located. Due to diffuse scatter, no pattern can be found within the brown hare population trends of region A.

At the interregional level only four out of five derived population trend samples for both hare species were reasonably large enough for further statistical analysis. Thus, the brown hare samples from region B ($n=3$) and region D (most of Skåne County) were excluded. The nonparametric Levene's test described the frequency distributions of the four selected samples as dissimilar. Despite this violation of the Kruskal-Wallis assumption of distribution similarity, the test statistic was computed arguing that the included right

skewed brown hare sample from region A and outliers in the mountain hare samples caused the differences. The Kruskal-Wallis H test ($H=21.463$; $df=3$; $p<.000$) revealed very highly significant differences between at least one pair of the group mean ranks. The post-hoc Tukey HSD equation uncovered the minimal difference to be $HSD=20.584$. It is thus statistically verified that mountain hares from region A decreased at higher rates ($p<.000$) than hares from all other parts of the study area, cf. Table 2. Further, it can be reported that mountain hares from region B and C as well as brown hares from region A have similar group mean ranks indicating the population decline in these distribution regions to be alike.

Table 2: Summarizing statistics and group mean ranks of the derived samples of hare population trend estimates b_{ts} for each distribution region during the period 1996-2010.

No.	Region	<i>Lepus sp.</i>	n	Distribution	Median	Mean	SE	Mean rank
1	A	<i>timidus</i>	16	ln-normal	-0.113	-0.118	0.011	15.59**
2	A	<i>europaeus</i>	16	right skewed	-0.066	-0.061	0.007	43.69
3	B	<i>timidus</i>	14	ln-bimodal	-0.053	-0.060	0.006	46.25
4	B	<i>europaeus</i>	3		0.013	0.013		
5	C	<i>timidus</i>	27	ln-normal	-0.070	-0.065	0.006	40.93
6	D	<i>europaeus</i>	1		-0.074	-0.074		

** - very highly significant ($p<.000$) difference to all other group mean rank values.

Hunting bag data reliability

For Finland the wildlife triangle indices (x_2) were regressed on hunting bag records per 10 km² (x_1) as lumped samples containing mixed time series from all hunting districts (cf. Appendix pp. IV, V). The expected positive interdependency of these two census methods seems to be emerging for only two species, viz. mountain hares ($R^2 \text{ adj.} = .497$; $F<.000$; $x_2=14.069+.72x_1$) and red foxes ($R^2 \text{ adj.} = .466$; $F<.000$; $x_2=1.483+1.865x_1$). Nevertheless, the residual scatterplots and the insignificant p-values for both regression line coefficients do not allow entirely accepting the model in either case. The linear regression analysis for brown hares has clearly no predictive power. Apart from numerous zero values in the tracking index data, the eye-fitted line on the scatter plot describes a rather bell-shaped curve peaking at around $x_1=6$ brown hares/10 km².

In Fig. 5 I present one possible approach to standardize the hare species HBD by the roughly estimated number of pedigreed "hare dog" pups at the national scale for Sweden. Surprisingly, the produced $CPUE$ time series for mountain hares appears to be almost detrended for the period 1996-2010 and thus relieving the constant decline in the uncorrected HBD. At the meanwhile, the brown hare curve shows even a constant positive trend over the whole time period (see also Appendix p.V).

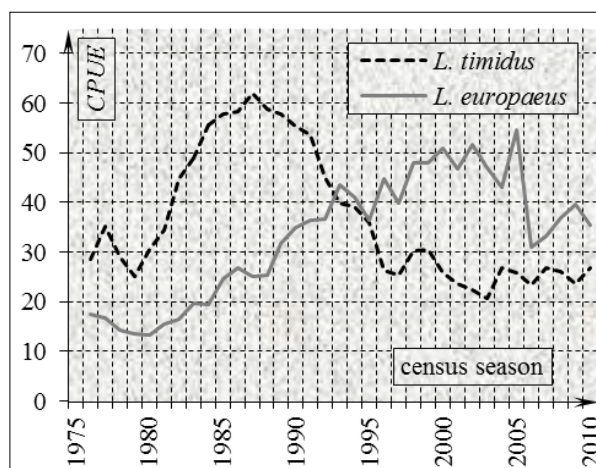


Fig. 5: Mountain hare and brown hare fluctuations as $CPUE$ time series for Sweden at the national scale from 1975 to 2010. The graphs show the original HBD divided by the measure of effort in number of pedigreed "hare dog" pups.

Discussion

During the period from 1996 to 2010 mountain hares throughout Fennoscandia had decreasing population trends (in 95% of all sample units); even after the deterministic population decline in Sweden during the 1980's and even within Pohjois-Savo, where overall most mountain hares were harvested on average. Interregionally, the significantly lowest negative population growth in this species occurred in heath-hares of southern Sweden (region A) de-culminating within a distinct zone around the 58° N latitude. Within southern and central Finland (region B) mountain hare population trends appear in two clusters with sharper decreasing trends in north-western hunting districts. Red fox population trend estimates were mostly positive (53%), but in Sweden least so between the 56.8° and 61.3° N latitudes. Highest median hunting bags for this species were recorded for the hunting district of Varsinais-Suomi as well as Södermanland and Skåne County. Within the latter, most brown hares were harvested during the same time period. However, this species was also diminishing in Sweden, though at similar rates as mountain hares did in arctic and boreal Fennoscandia (regions B and C). Historically (1960-2010), the majority of the correlated time series sequences of red foxes and either hare species at the county scale was insignificant (71% of all possible correlates). The absence of correlations for southern Sweden between red fox and brown hare population density indices during 1984-1992 and between red foxes and mountain hares during 2003-2010 is most notable.

Although widely used within wildlife ecology, the credibility of hunting bag records as an index of change in population size is debatable ([Winterhalder 1980](#), [Cattadori et al. 2003](#), [Jarnemo and Liberg 2005](#)). The linear regression of the wildlife triangle data on HBD densities for Finland revealed that both census methods are supposedly prone to considerable influence of sample error. Especially, the result for brown hares was unexpected, though most bias in this case may arise from the wildlife triangle data (cf. Appendix p. IV). As outlined by Moleón et al. ([2012](#)) it is scientifically more informative to standardize HBD by a measure of hunting effort. However, apart from the difficulty to establish such a measure nation-wide, it also harbors the risk of introducing other forms of bias. The presented number of pedigreed "hare dog" pups e.g. (cf. Fig. 5) appears to be a less useful estimator of hunting effort because it does not point out regional differences of the dogs in use, if at all deployed in hunting purposes. Besides, socio-economic factors, functional responses as well as changes in hunting behavior may blur the outcome even further. Despite these problems, I consider the decline in mountain hare HBD being partially explained by reduced hunting effort, since this species is almost exclusively hunted with "hare dogs". The positive population trend indices for red foxes and the still high numbers of brown hares until 1994, however, cast doubt on this presumption, because mountain hare hunt with scent hounds is a highly valued hunting method, also within southern Sweden. There might be a widely spread cautionary principle, to not overharvest an already lower local mountain hare population, which in turn lead to further reduction in hunting bag records. For a boreal study area in Västerbotten County, Dahl ([2005](#)) estimated the percentage of surviving mountain hares that fell victim to hunting before their first reproduction, to be 25%. Thus, the smaller the censused population the less reliable gets this invasive inventory method.

When loosening assumption (2), the comparability of HBD from different origins is indeed questionable due to profound dissimilarities within the data collection of the census regimes (Jonas Kindberg 2013, pers. comm.). Thus, the high median values of harvested mountain hares within Finland (cf. Fig. 4) are possibly lower in reality. Nonetheless, there are also plausible ecological and traditional reasonings that would explain these results. Firstly, the

continental influence on the climate may be beneficial. Secondly, the diversity of inland water bodies in south-central Finland might be impedimental to forestry logistics, supports the growth of important deciduous shelter and winter food plants, such as goat willow *Salix caprea* L. 1758, European aspen *Populus tremula* L. 1758 as well as birches *Betula spp.* ([Jason and Palo 1991](#)) and supposedly creates more suitable habitats favoring leveret survival ([Krebs et al. 2002](#)). Thirdly, small game hunt may be more popular in Finland than in Scandinavia. Concerning the population trend analysis, the comparison across national borders should, however, be more tangible given constant sample errors through time within each census regime.

As Lindström et al. ([1986](#)) point out, a considerable number of predators present in Fennoscandia forage on both hare species, but none appears to be specialized (cf. Table 1). In many cases however, hares are ranked second or third important food resource regardless of season, micro habitat or sample size. The food niche width of the predator species and the type of percentage chosen to represent the dietary proportions are decisive when evaluating the overall importance of a prey species ([Cavallini and Volpi 1995](#)). Only Nyström et al. ([2006](#)) applied DNA species assignment. Furthermore, it becomes evident that red fox predation on hares seems to vary from temporarily almost entirely relying on hares in island ecosystems ([Angerbjörn 1989](#)) to virtually neglecting them as a food resource during microtine peak years ([Lindström 1982](#), [Angelstam et al. 1984](#)). Notably, Panek ([2013](#)) found that red fox predation rates also can greatly change over longer periods of time. While mesopredators (i.a. red foxes) and most raptors focus on rodents or birds, larger sized carnivores favor ungulate prey. If the primary food resource for any reason gets less abundant or accessible, hares may become important as secondary prey (see Table 1). At the local scale, this alternative prey hypothesis has been substantiated for red foxes ([Angelstam et al. 1984](#), [Kjellander and Nordström 2003](#)). In this study, however, the correlation analysis on red fox and either hare species for Sweden only give little to no evidence for synchronized predator and alternative prey fluctuations. These findings are in line with those of Kauhala and Helle ([2000](#)), who report that less than half of the correlates between red fox and mountain hare populations were significant. In contrast, the insights on red fox predation as influential cause of hare mortality ([Dahl 2005](#)) are less reflected. Furtheron, red fox and mountain hare populations have been reported being negatively crosscorrelated with a time lag of one year ([Small et al. 1993](#)) or even completely detached from one another ([Kauhala et al. 1999](#)). For northern Sweden, a synchrony pattern first shows through in the pooled time series contrasting the matched snowshoe hare periodicity also over abroad areas ([Krebs et al. 2001](#)). This would indicate that the extrinsic factor of microtine population cycles is conveyed onto mountain hares via red foxes ([Hörnfeldt et al. 1986](#)). In contrary, the similarly positively correlated brown hare and red fox time series from region A might rather be explained by other factors, e.g. adverse winter conditions and/or primary prey accessibility. Additionally, Hörnfeldt et al. ([2005](#)) conclude that milder and wetter winters since the early 1970's are causing microtine cycles to fade out even in northern Sweden. This is mirrored by the HBD for mountain hares from region C'. The limiting impact of red foxes on small game is described as becoming evident ([Lindström et al. 1994](#)) during the sarcoptic mange outbreak ([Mörner 1992](#)). This view is partially substantiated by the numerous negative correlation coefficients found in this study. Astonishingly, time series at the county scale south to the 58° N latitude leave room to assume that red foxes were (1) a participating predator species causing the mountain hare populations to crash, (2) preferred on mountain hares over brown hares and (3) caused the mountain hare populations to drop below a crucial level.

In theory, Gause's competitive exclusion principle requires five key conditions to be met. If noninterbreeding populations of two closely related species live in sympatry and have a considerable niche overlap than the species with only slightly more effective reproductive success will eventually displace their competitor ([Hardin 1960](#)). In this case, I suggest, that everytime hybridization with merely unidirectional gene introgression occurs, the reproductive output of mountain hares will get even further reduced. Contrastingly, the sympatric niche overlap requirement appears only weakly fulfilled. However, summer diet, shelter ([Hiltunen 2003](#)) and access to winter food resorts certainly fall within the needs of both species. Interestingly, Lind ([1963](#)) documents behavioral adaptations in mountain hares close to brown hares, which designate the interaction between the two hare species to be competitive. In this respect, it is noteworthy that brown hares obviously used the opportunity, e.g. during long lasting high population sizes in region A until 1994 (see Appendix p. II), to disperse further into the clear-cut coniferous forests ([Jansson and Pehrson 2007](#)) and thus increase encounter rates with mountain hares. An extreme example of a scenario to expect also for other agricultural areas (e.g. Gotland and Södermanland) may have already taken place in region D, where heath-hares went extinct ([Thulin 2003](#)). Putting the decline in brown hares from region A and D into perspective, Schmidt et al. ([2004](#)) conclude for similarly decreasing populations in Denmark, that negative associations with red fox population dynamics and shifts in agriculture towards the cultivation of winter cereals are not reversed by the beneficial impact of milder winters. It is possible that other causative factors overshadow positive brown hare trends benefiting from the interactions with mountain hares. The failure to describe the population trends of red foxes and brown hares for region B is probably due to too high variances or multiple trends within the hunting bag time series. Judged from visual inspection, these species have most likely constant or weakly fluctuating population dynamics throughout the period 1996-2010. Thus, it might be legitimate to state that mountain hare decline is linked to stable brown hare populations. The converse spatial HBD density pattern for this region would support this statement (cf. Fig. 4). In contradiction, the group mean ranks for region C and B are too similar to assume the influence of brown hares on mountain hares overshadowing other working mechanisms.

Given the various ecosystems within Fennoscandia, it is most reasonable to expect different mechanisms causing the assumed declines in mountain hares. The factors slowing down mountain hare population growth in region A during the beginning sarcoptic mange outbreak appear to have been more numerous or intense than in region C'. Here, the diminishing impact of red foxes triggered an abrupt positive population growth as in brown hares of region A (cf. Table 2, Appendix p. II). In general, opportunist predation, pathogen impact and also competition as single factors are certainly density dependent. Therefore, I postulate that multiple factors were involved in the population downturn, specifically in heath-hare populations below the 58° N latitude. Spatially roughly fitting (cf. Fig. 3), the mesopredator release hypothesis finds partially support by the findings in this study. Interestingly, highest mountain hare HBD densities in Finland also overlap with densest stationary wolf *Canis lupus* L. 1758 abundance. Besides wolves, also lynxes *Lynx lynx* L. 1758 exhibit intraguild predation ([Elmhagen et al. 2010](#)), which possibly led to less positive population growth in red foxes and thus alleviating the negative mountain hare trends in central Sweden. One could easily redraft this theory into a megaherbivore release hypothesis and expect the potential negative competitive impact of large herbivores on mountain hares ([Hulbert and Andersen 2001](#)) to decrease when apex predators are present. With a broader ecological view, apparent competition species assemblages ([DeCesare et al. 2009](#)) deserve more scientific attention; be it the current situation on Gotland, where

Golden eagles *Aquila chrysaetos* L. 1758 are supported by other prey, i.a. brown hares, and might force heath-hares towards extinction, or be it the potential spread of viral diseases like European Brown Hare Syndrome (EBHS) ([Syrjälä et al. 2005](#)) transmitted by brown hares into mountain hare populations of Sweden during the time period 1988-1995. During this phase of most severe mountain hare decline south to the 58° N, the ecological role of the recovering red fox populations remains unclear. Thus, I suggest that predation (likely also by red foxes), pathogens, and exploitation competition may have forced mountain hares under a crucial population density. The expanding brown hare populations might have had a detrimental function in this downturn. If the trends between 1996-2010 revealed in this study describe the actual population size history of mountain hares in southern Sweden, it will be an utmost hard struggle to recover, considering the short and danger-filled dispersal distances ([Dahl and Willebrand 2005](#)), the discontinuous, highly variable landscape with a high probability of the Allee effect, and a hybridizing congener that seems to be ready to ecologically replace them ([Thulin 2003](#), [Acevedo et al. 2012](#), [Hof et al. 2012](#)).

Conclusion

In summary the results of this study are ambivalent concerning both working hypotheses. On the one hand, only partial evidence was revealed for the limiting impact of red fox predation on mountain hares. In particular, the correlation analysis did not show how red foxes might affect hare species during the nonepizootic ecosystem state. On the other hand, the trend analysis described southern Sweden as the region, where mountain hares do still decline most rapidly. However, this pattern appears to be less explained by brown hare population trends, which also decrease in Sweden. In parapatric Finland, assumed stable brown hare population dynamics lead obviously not to more severe declines in mountain hares than in northern Sweden. It can, however, be stated that both hare species occur in converse abundances, which in turn could also be a simple function of habitat suitability. The downfall of heath-hare populations in southern Sweden was triggered during the sarcoptic mange event. Predation might have had an important influence, but which role red foxes played is uncertain. The delayed downturn in brown hares of the same region indicates either higher reproductive and/or survival rates but possibly also a preference by red foxes for mountain hares. In general, habitat quality, i.e. the availability of deciduous trees, appears to be the most decisive factor to cope with the multitude of threats, which hares have to face. Apparent competition and exploitation competition with megaherbivores have supposedly unrecognized importance and the negative influence on mountain hares might get alleviated by reestablishing apex predators. The hunting bag data reliability analysis allows only restricted confidence into inferred information presented in this study.

The precision of future hunting bag data should be tested by means of establishing or embedding alternative census methods. Spatially of highest interest are parapatric Skåne, Gotland, Södermanland, Östergötland and Västra Götaland County. Also, the development of e.g. DNA-based monitoring techniques to distinguish between the hare species in predator diet composition studies should be developed. Furthermore, the direct interaction between brown and mountain hares needs more scientific attention. Predominantly, the mating ecology in sympatric hare populations should be investigated.

Management implications

From a management perspective, hares in Fennoscandia have a low societal conflict potential but are of importance as a game species and a vivid symbol of the north. To improve the informative value of the hunting bag records a measure of effort, e.g. time, is necessary. For analyzing population ecological questions, it would also be beneficial to report color morph, approximate age and sex of the harvested individuals. Alternative census methods (e.g. hare observations or pellet counts) could be included into those that are already conducted on other wildlife species. If the trends in the hunting bag time series get substantiated, hunting pressure should be controlled in a more organized manner. According to the virtual absence of mountain hares in Skåne, but also in Gotland County, the regional red-listing of mountain hares is likely overdue. In case climate warming leads to a broader range shift in mountain hares, it might get inevitable to consider this ecological process both in hunting and wildlife management.

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References

- Acevedo, P., A. Jimenez-Valverde, J. Melo-Ferreira, R. Real, and P. C. Alves. 2012. Parapatric species and the implications for climate change studies: a case study on hares in Europe. *Global Change Biology* **18**:1509-1519.
- Alves, P. C., N. Ferrand, and K. Hackländer. 2008. *Lagomorph Biology - Evolution, Ecology, and Conservation*. Page 4. Springer Berlin Heidelberg, New York City.
- Angelstam, P., E. Lindström, and P. Widén. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia* **62**:199-208.
- Angerbjörn, A. 1989. Mountain hare populations on islands: effects of predation by red fox. *Oecologia* **81**:335-340.
- Angerbjörn, A. and J. E. C. Flux. 1995. *Lepus timidus*. *Mammalian species*:1-11.
- Ansorge, H., G. Kluth, and S. Hahne. 2006. Feeding ecology of wolves *Canis lupus* returning to Germany. *Acta Theriologica* **51**:99-106.
- Arnold, S., J. Avise, J. Ballou, J. Eldridge, and D. Flemming. 1991. Genetic management considerations for threatened species with a detailed analysis of the Florida panther (*Felis concolor coryi*). Pages 1-20 *Genetic management considerations for threatened species with a detailed analysis of the Florida panther*. USFWS, Washington, DC.
- Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L. Lindsey, and K. C. Maguire. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* **471**:51-57.
- Bauer, M. 2010. Michael Bauer Research GmbH. Europe NUTS 3 Demographics (nuts3.sdc), Vector digital data. ESRI® Redlands, California, USA.
- Bergengren, A. 1969. On genetics, evolution and history of distribution of the heath-hare, a distinct population of the Arctic hare, *Lepus timidus* Lin. *Swedish Wildlife Research - Viltrevy* **6**:381-460.
- Björck, S. 1995. A review of the history of the Baltic Sea, 13.0-8.0 ka BP. *Quaternary International* **27**:19-40.
- Brand, C. J. and L. B. Keith. 1979. Lynx demography during a snowshoe hare decline in Alberta. *The Journal of Wildlife Management*:827-849.
- Brodersen, C. 2005. Arctic climate impact assessment. 0521865093, Norsk Polarinstitutt, Tromsø, Cambridge University Press Cambridge.
- Carlsson, N. O. L., J. M. Jeschke, N. Holmqvist, and J. Kindberg. 2010. Long-term data on invaders: when the fox is away, the mink will play. *Biological Invasions* **12**:633-641.
- Cattadori, I. M., D. T. Haydon, S. J. Thirgood, and P. J. Hudson. 2003. Are indirect measures of abundance a useful index of population density? The case of red grouse harvesting. *Oikos* **100**:439-446.
- Cavallini, P. and T. Volpi. 1995. Biases in the analysis of the diet of the red fox *Vulpes vulpes*. *Wildlife Biology* **1**:243-248.
- Ceballos, G. and P. R. Ehrlich. 2002. Mammal population losses and the extinction crisis. *Science* **296**:904-907.
- Dahl, F. 2005. Life and death of the mountain hare in the boreal forest of Sweden. PhD Thesis, *Acta Universitatis Agriculturae Sueciae* **48**:1-37.
- Dahl, F. and T. Willebrand. 2005. Natal dispersal, adult home ranges and site fidelity of mountain hares *Lepus timidus* in the boreal forest of Sweden. *Wildlife Biology* **11**:309-317.
- DeCesare, N. J., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2009. Endangered, apparently: the role of apparent competition in endangered species conservation. *Animal Conservation* **13**:353-362.

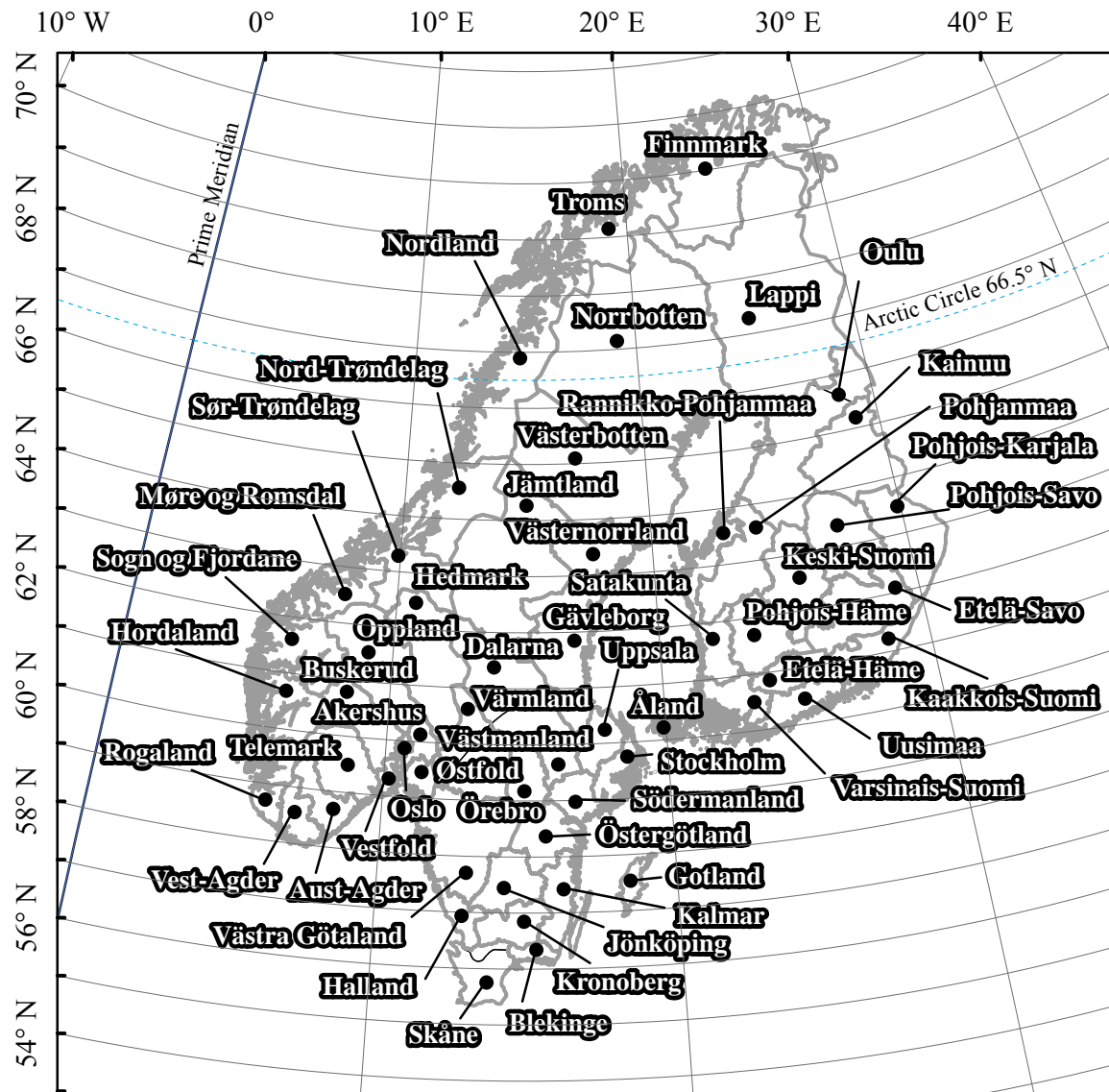
- Elmhagen, B., G. Ludwig, S. P. Rushton, P. Helle, and H. Lindén. 2010. Top predators, mesopredators and their prey: Interference ecosystems along bioclimatic productivity gradients. *Journal of Animal Ecology* **79**:785-794.
- Flux, J. E. C. 1981. Reproductive strategies in the genus *Lepus*. Pages 155-177 in *Proceedings of the World Lagomorph Conference* (K. Myers and CD MacInnes, eds.). University of Guelph, Guelph, Ontario, Canada.
- Fredsted, T., T. Wincentz, and P. Villesen. 2006. Introgression of mountain hare (*Lepus timidus*) mitochondrial DNA into wild brown hares (*Lepus europaeus*) in Denmark. *BMC Ecology* **6**.
- Geiser, F. and C. Turbill. 2009. Hibernation and daily torpor minimize mammalian extinctions. *Naturwissenschaften* **96**:1235-1240.
- Gustavsson, I. and C. O. Sundt. 1965. Anwendung von künstlicher Befruchtung bei der Hybridisierung von zwei Hasenarten in German. *Zeitschrift für Jagdwissenschaft* **11**:155-158.
- Hardin, G. 1960. The competitive exclusion principle. *Science* **131**:1292-1297.
- Helldin, J. O. 1999. Diet, body condition, and reproduction of Eurasian pine martens *Martes martes* during cycles in microtine density. *Ecography* **22**:324-336.
- Hewitt, C. G. 1921. *The conservation of the wildlife of Canada*. Scribner's Sons, New York.
- Hiltunen, M. 2003. Feeding intensity of mountain hares (*Lepus timidus*) during winter in Finland. *Mammalian Biology* **68**:48-52.
- Hof, A. R., R. Jansson, and C. Nilsson. 2012. Future climate change will favour non-specialist mammals in the (Sub)Arctics. *PLoS ONE* **7**.
- Hubbs, C. L. 1955. Hybridization between fish species in nature. *Systematic zoology* **4**:1-20.
- Hulbert, I. A. and R. Andersen. 2001. Food competition between a large ruminant and a small hindgut fermentor: The case of the roe deer and mountain hare. *Oecologia* **128**:499-508.
- Hörnfeldt, B., T. Hipkiss, and U. Eklund. 2005. Fading out of vole and predator cycles? *Proceedings of the Royal Society B: Biological Sciences* **272**:2045-2049.
- Hörnfeldt, B., O. Löfgren, and B. G. Carlsson. 1986. Cycles in voles and small game in relation to variations in plant production indices in Northern Sweden. *Oecologia* **68**:496-502.
- Iason, G. R. and R. T. Palo. 1991. Effects of birch phenolics on a grazing and a browsing mammal: A comparison of hares. *Journal of Chemical Ecology* **17**:1733-1743.
- Inchausti, P. and L. R. Ginzburg. 2009. Maternal effects mechanism of population cycling: a formidable competitor to the traditional predator-prey view. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**:1117-1124.
- IUCN. 2013. *Red List of Threatened Species*. Version 2013.2. International Union for Conservation of Nature.
- Jaarola, M., H. Tegelström, and K. Fredga. 1999. Colonization history in Fennoscandian rodents. *Biological Journal of the Linnean Society* **68**:113-127.
- Jansson, G. and A. Pehrson. 2007. The recent expansion of the brown hare (*Lepus europaeus*) in Sweden with possible implications to the mountain hare (*L. timidus*). *European Journal of Wildlife Research* **53**:125-130.
- Jarnemo, A. and O. Liberg. 2005. Red fox removal and roe deer fawn survival-a 14-year study. *Journal of Wildlife Management* **69**:1090-1098.
- Kauhala, K. and P. Helle. 2000. The interactions of predator and hare populations in Finland - A study based on wildlife monitoring counts. *Annales Zoologici Fennici* **37**:151-160.

- Kauhala, K. and P. Helle. 2007. Mountain hares in sharp decline (Metsäjäniskanta pienentynyt voimakkaasti) in Finnish with English abstract., *Riista- ja kalatalous - Selvityksiä* 3/2007 12 s., Riista- ja kalatalouden tutkimuslaitos RKTL., Helsinki.
- Kauhala, K., P. Helle, E. Helle, and J. Korhonen. 1999. Impact of predator removal on predator and mountain hare populations in Finland. *Annales Zoologici Fennici* **36**:139-148.
- Kauhala, K., P. Laukkanen, and I. Rége. 1998. Summer food composition and food niche overlap of the raccoon dog, red fox and badger in Finland. *Ecography* **21**:457-463.
- Kjellander, P. and J. Nordström. 2003. Cyclic voles, prey switching in red fox, and roe deer dynamics - A test of the alternative prey hypothesis. *Oikos* **101**:338-344.
- Koskela, A., I. Kojola, J. Aspi, and M. Hyvärinen. 2013. The diet of breeding female wolverines (*Gulo gulo*) in two areas of Finland. *Acta Theriologica* **58**:199-204.
- Krebs, C. J., R. Boonstra, S. Boutin, and A. R. E. Sinclair. 2001. What drives the 10-year cycle of snowshoe hares? *BioScience* **51**:25-35.
- Krebs, C. J., T. N. Zimmerling, C. Jardine, K. A. Trostel, A. J. Kenney, S. Gilbert, and E. J. Hofer. 2002. Cyclic dynamics of snowshoe hares on a small island in the Yukon. *Canadian journal of zoology* **80**:1442-1450.
- Lepiksaar, J. 1986. The Holocene history of theriofauna in Fennoscandia and Baltic countries. *Striae* **24**:51-70.
- Lind, E. A. 1963. Observations on the mutual relationship between the snow hare (*Lepus timidus*) and the field hare (*L. europaeus*). *Suomen Riista* **16**:128-135.
- Lindén, H., E. Helle, P. Helle, and M. Wikman. 1996. Wildlife triangle scheme in Finland: methods and aims for monitoring wildlife populations. *Finnish Game Research* **49**:4-11.
- Lindström, E. 1982. Population ecology of the red fox (*Vulpes vulpes* L.) in relation to food supply. University of Stockholm Sweden.
- Lindström, E., H. Andrén, P. Angelstam, and P. Widen. 1986. Influence of predators on hare populations in Sweden - A critical review. *Mammal Review* **16**:151-156.
- Lindström, E. R., H. Andrén, P. Angelstam, G. Cederlund, B. Hörnfeldt, L. Jäderberg, P. A. Lemnell, B. Martinsson, K. Sköld, and J. E. Swenson. 1994. Disease reveals the predator: Sarcoptic mange, red fox predation, and prey populations. *Ecology* **75**:1042-1049.
- Liow, L. H., M. Fortelius, K. Lintulaakso, H. Mannila, and N. C. Stenseth. 2009. Lower Extinction Risk in Sleep or Hide Mammals. *The American Naturalist* **173**:264-272.
- Lönnberg, E. 1905. On hybrids between *Lepus timidus* L. & *Lepus europaeus* Pall. from southern Sweden. *Proceedings of Zoological Society of London*, 1, 278-287.
- Lönnberg, E. 1908. Några villebrådsarters nutida utbredning i Skåne in Swedish. *Svenska Jägarförbundets Tidskrift* **46**:7-16.
- Melo-Ferreira, J., P. Boursot, F. Suchentrunk, N. Ferrand, and P. C. Alves. 2005. Invasion from the cold past: Extensive introgression of mountain hare (*Lepus timidus*) mitochondrial DNA into three other hare species in northern Iberia. *Molecular Ecology* **14**:2459-2464.
- Mills, L. S., M. Zimova, J. Oyler, S. Running, J. T. Abatzoglou, and P. M. Lukacs. 2013. Camouflage mismatch in seasonal coat color due to decreased snow duration. *Proceedings of the National Academy of Sciences* **110**:7360-7365.
- Mitchell-Jones, A. J., G. Amori, W. Bogdanowicz, B. Krystufek, P. J. H. Reijnders, F. Spitzenberger, M. Stubbe, J. B. M. Thissen, V. Vohralik, and J. Zima. 1999. The atlas of European mammals.
- Moleón, M., P. Almaraz, and J. A. Sánchez-Zapata. 2012. Inferring ecological mechanisms from hunting bag data in wildlife management: A reply to Blanco-Aguilar et al. (2012). *European Journal of Wildlife Research* **59**:599-608.

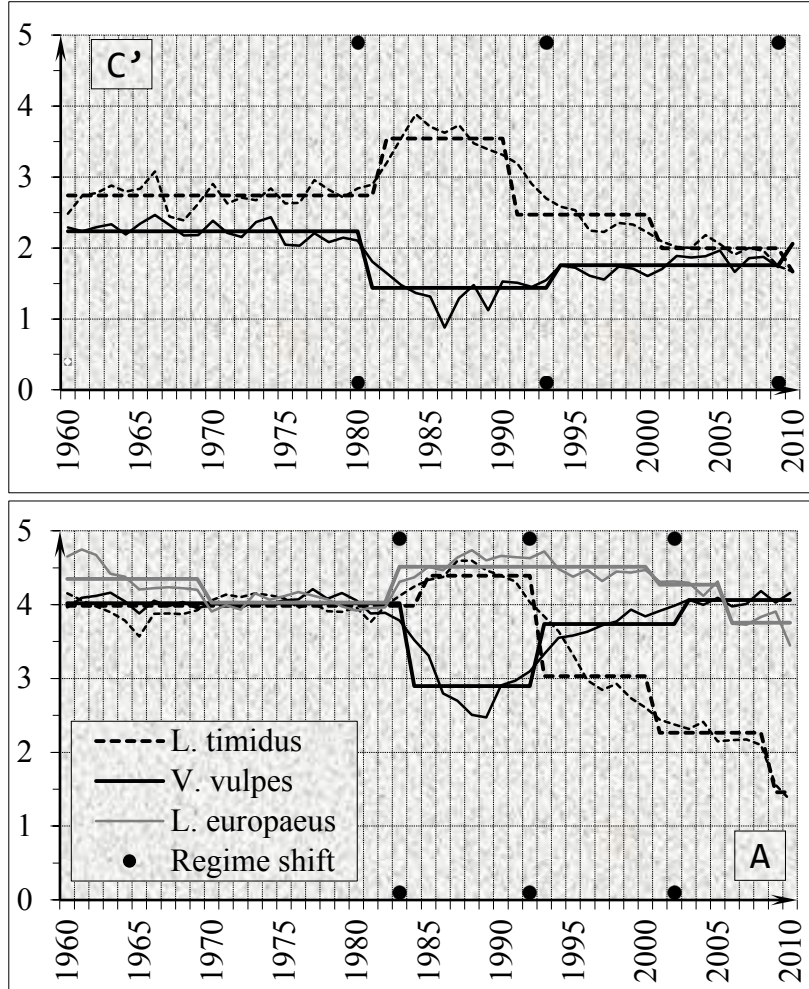
- Müller, S. 2006. Diet composition of wolves (*Canis lupus*) on the Scandinavian Peninsula determined by scat analysis. MSc Thesis, School of Forest Science and Resource Management, Technical University of München, Germany.
- Mörner, T. 1992. Sarcoptic mange in Swedish wildlife. *OIE Revue Scientifique et Technique* **11**:1115-1121.
- Newey, S.-J. 2005. Population fluctuations in mountain hares: a role for parasites? PhD Thesis, *Acta Universitatis Agriculturae Sueciae* **26**:1-40.
- Nowak, R. M., E. P. Walker, F. Warnick, S. E. Hamlet, K. I. Lange, M. A. Davis, H. E. Uible, P. F. Wright, and J. L. Paradiso. 1975. Walker's Mammals of the world. Pages 1715 ff, 6th ed. Volume 2 of 2.
- Nyström, J., J. Ekenstedt, A. Angerbjörn, L. Thulin, P. Hellström, and L. Dalén. 2006. Golden Eagles on the Swedish mountain tundra - Diet and breeding success in relation to prey fluctuations. *Ornis Fennica* **83**:145.
- Nývtlová-Fisáková, M. 2000. Menu of Gravettian people from southern Moravia. *Acta Universitatis Carolinae. Medica* **41**:37.
- Odden, J., J. D. C. Linnell, and R. Andersen. 2006. Diet of Eurasian lynx, *Lynx lynx*, in the boreal forest of southeastern Norway: The relative importance of livestock and hares at low roe deer density. *European Journal of Wildlife Research* **52**:237-244.
- Panek, M. 2013. Long-term changes in the feeding pattern of red foxes *Vulpes vulpes* and their predation on brown hares *Lepus europaeus* in western Poland. *European Journal of Wildlife Research*:1-6.
- Pedersen, S. and H. C. Pedersen. 2012. The population status of mountain hare in Norway - state of knowledge (Bestandssituasjonen for hare i Norge - en kunnskapsstatus) in Norwegian with English abstract. NINA Rapport 886. 41 s., Norsk institutt for naturforskning, Trondheim.
- Pulliainen, E. 1981. Winter diet of *Felis lynx* in SE Finland as compared with the nutrition of other northern lynxes. *Zeitschrift für Säugetierkunde*. **46**:249-259.
- Reif, V., R. Tornberg, S. Jungell, and E. Korpimäki. 2001. Diet variation of common buzzards in Finland supports the alternative prey hypothesis. *Ecography* **24**:267-274.
- Rhymer, J. M. and D. Simberloff. 1996. Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics* **27**:83-109.
- Rodionov, S. N. 2004. A sequential algorithm for testing climate regime shifts. *Geophysical Research Letters* **31**.
- Sándor, A. D. and D. T. Ionescu. 2009. Diet of the eagle owl (*Bubo bubo*) in Braşov, Romania. *North-Western Journal of Zoology* **5**:170-178.
- Schmidt, N. M., T. Asferg, and M. C. Forchhammer. 2004. Long-term patterns in European brown hare population dynamics in Denmark: Effects of agriculture, predation and climate. *BMC Ecology* **4**.
- Schröder, J., T. Soveri, H. A. Suomalainen, L. A. Lindberg, and W. van der Loo. 1987. Hybrids between *Lepus timidus* and *Lepus europaeus* are rare although fertile. *Hereditas* **107**:185-189.
- Sidorovich, V. E., A. A. Sidorovich, and I. V. Izotova. 2006. Variations in the diet and population density of the red fox *Vulpes vulpes* in the mixed woodlands of northern Belarus. *Mammalian Biology* **71**:74-89.
- Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. 312 pp. McGraw-Hill, New York.
- Simberloff, D. 1996. Hybridization between native and introduced wildlife species: importance for conservation. *Wildlife Biology* **2**:143-150.

- Small, R. J., V. Marcström, and T. Willebrand. 1993. Synchronous and nonsynchronous population fluctuations of some predators and their prey in central Sweden. *Ecography* **16**:360-364.
- Smith, R. K., N. Vaughan Jennings, and S. Harris. 2005. A quantitative analysis of the abundance and demography of European hares *Lepus europaeus* in relation to habitat type, intensity of agriculture and climate. *Mammal Review* **35**:1-24.
- Stocker, T., Q. Dahe, and G.-K. Plattner. 2013. Working group I contribution to the IPCC fifth assessment report (AR5), Climate change 2013: The physical science basis. Stockholm.
- Syrjälä, P., M. Nylund, and S. Heinikainen. 2005. European brown hare syndrome in free-living mountain hares (*Lepus timidus*) and European brown hares (*Lepus europaeus*) in Finland 1990-2002. *Journal of wildlife diseases* **41**:42-47.
- Taberlet, P., J. E. Swenson, F. Sandegren, and A. Bjärvall. 1995. Localization of a contact zone between two highly divergent mitochondrial DNA lineages of the brown bear *Ursus arctos* in Scandinavia. *Conservation Biology* **9**:1255-1261.
- Thulin, C.-G. 2003. The distribution of mountain hares *Lepus timidus* in Europe: A challenge from brown hares *L. europaeus*? *Mammal Review* **33**:29-42.
- Thulin, C.-G., M. Fang, and A. O. Averianov. 2006a. Introgression from *Lepus europaeus* to *L. timidus* in Russia revealed by mitochondrial single nucleotide polymorphisms and nuclear microsatellites. *Hereditas* **143**:68-76.
- Thulin, C.-G., M. Jaarola, and H. Tegelström. 1997. The occurrence of mountain hare mitochondrial DNA in wild brown hares. *Molecular Ecology* **6**:463-467.
- Thulin, C.-G., J. Stone, H. Tegelström, and C. W. Walker. 2006b. Species assignment and hybrid identification among Scandinavian hares *Lepus europaeus* and *L. timidus*. *Wildlife Biology* **12**:29-38.
- Thulin, C.-G. and H. Tegelström. 2002. Biased geographical distribution of mitochondrial DNA that passed the species barrier from mountain hares to brown hares (genus *Lepus*): An effect of genetic incompatibility and mating behaviour? *Journal of zoology* **258**:299-306.
- Thulin, C.-G., H. Tegelström, and K. Fredga. 2003. Haplotype diversity of mountain hare mtDNA among native mountain hares and introduced brown hares in Scandinavia. *Annales Zoologici Fennici* **40**:45-52.
- Tornberg, R. and A. Colpaert. 2001. Survival, ranging, habitat choice and diet of the Northern Goshawk *Accipiter gentilis* during winter in northern Finland. *Ibis* **143**:41-50.
- Tyson, R., S. Haines, and K. E. Hodges. 2010. Modelling the Canada lynx and snowshoe hare population cycle: The role of specialist predators. *Theoretical Ecology* **3**:97-111.
- Western, D. and M. C. Pearl. 1989. Conservation for the Twenty-first Century. Pages 37-41. Oxford University Press, New York, USA.
- Vik, J. O., C. N. Brinch, S. Boutin, and N. C. Stenseth. 2008. Interlinking hare and lynx dynamics using a century's worth of annual data. *Population Ecology* **50**:267-274.
- Winterhalder, B. P. 1980. Canadian fur bearer cycles and Cree-Ojibwa hunting and trapping practices. *American Naturalist*:870-879.

Appendix



Administrative nomenclature of counties for Norway and Sweden and hunting districts for Finland (State: 2013 onwards; Projected coordinate system: SWEREF 99 TM; Graticule: Decimal degrees, DD; References see text).



Natural logarithm of the sum of sample unit hunting bag densities ($\ln[\sum \text{HBD}/10\text{km}^2/\text{sample unit}]$; y-axis) for mountain hares, brown hares and red foxes from distribution region C' and A against census seasons 1960-2010. Bold linear graphs show the regime sequences per species as calculated by the STARS algorithm with a set cut-off length of $l=10$ years and a Huber weight equal to 1. Black dots demarcate corresponding regime shifts in the red fox density time series, which then were used in the Spearman rank correlation analysis to detect associations with hare population fluctuations.

No.	Region	Spatial ID	County name	<i>X</i>	<i>Y</i>	<i>n</i>	Period	<i>rs tim</i>	<i>p tim</i>	<i>rs eur</i>	<i>p eur</i>
1	C'	SE331	Västerbotten	635730	7196636	13	1981-1993	-0.73	.005	•	•
2	C'	SE331	Västerbotten	635730	7196636	16	1994-2009	0.499	.049	•	•
3	C'	SE321	Västernorrland	657271	7034187	13	1981-1993	-0.681	.010	•	•
4	C'	SE322	Jämtland	474820	7032335	21	1960-1980	0.663	.001	•	•
5	C'	SE313-A	Gävleborg	551736	6833798	13	1981-1993	-0.769	.002	•	•
6	A	SE121	Uppsala	643036	6659293	9	1984-1992	-0.932	.000	•	•
7	A	SE110	Stockholm	697765	6636572	9	1984-1992	-0.73	.026	•	•
8	A	SE125	Västmanland	567407	6620057	9	1984-1992	-0.954	.000	•	•
9	A	SE125	Västmanland	567407	6620057	7	2003-2010	•	•	0.929	.003
10	C'	SE311-A	Värmland	342159	6617789	13	1981-1993	-0.637	.019	•	•
11	A	SE124	Örebro	498402	6579517	24	1960-1983	•	•	0.791	.000
12	A	SE124	Örebro	498402	6579517	9	1984-1992	-0.866	.003	0.772	.015
13	A	SE124	Örebro	498402	6579517	10	1993-2002	-0.648	.043	•	•
14	A	SE122	Södermanland	593410	6551146	24	1960-1983	•	•	0.538	.007
15	A	SE122	Södermanland	593410	6551146	10	1993-2002	-0.903	.000	-0.673	.033
16	A	SE122	Södermanland	593410	6551146	7	2003-2010	•	•	0.929	.003
17	A	SE123	Östergötland	538284	6469121	24	1960-1983	•	•	0.498	.013
18	A	SE232	Västra Götaland	375469	6465495	9	1984-1992	-0.817	.007	•	•
19	A	SE232	Västra Götaland	375469	6465495	10	1993-2002	-0.927	.000	-0.915	.000
20	A	SE214	Gotland	710456	6377018	24	1960-1983	-0.739	.000	-0.686	.000
21	A	SE214	Gotland	710456	6377018	7	2003-2010	•	•	0.857	.014
22	A	SE211	Jönköping	464432	6376755	9	1984-1992	-0.862	.003	•	•
23	A	SE211	Jönköping	464432	6376755	10	1993-2002	-0.903	.000	-0.806	.005
24	A	SE213	Kalmar	562993	6344864	24	1960-1983	0.674	.000	0.733	.000
25	A	SE213	Kalmar	562993	6344864	9	1984-1992	-0.696	.037	•	•
26	A	SE213	Kalmar	562993	6344864	10	1993-2002	-0.9	.000	-0.646	.043
27	A	SE231	Halland	369235	6314570	9	1984-1992	-0.812	.008	•	•
28	A	SE212	Kronoberg	473516	6297159	24	1960-1983	0.66	.000	0.584	.003
29	A	SE212	Kronoberg	473516	6297159	9	1984-1992	-0.975	.000	•	•
30	A	SE212	Kronoberg	473516	6297159	10	1993-2002	-0.9	.000	-0.863	.001
31	A	SE212	Kronoberg	473516	6297159	7	2003-2010	•	•	0.893	.007
32	A	SE224	Skåne	514157	6240625	24	1960-1983	-0.453	.026	•	•
33	A	SE224	Skåne	514157	6240625	9	1984-1992	-0.72	.029	-0.71	.032
34	A	SE221	Blekinge	514157	6240625	9	1984-1992	•	•	-0.689	.040
35	A	SE221	Blekinge	514157	6240625	10	1993-2002	-0.657	.039	•	•

Spearman rank correlates of population indices without time lags

1	C'	SE331	Västerbotten	635730	7196636	21	1960-1980	-0.443	.044	•	•
2	C'	SE322	Jämtland	474820	7032335	21	1960-1980	-0.616	.003	•	•
3	A	SE121	Uppsala	643036	6659293	24	1960-1983	-0.409	.047	•	•
4	A	SE110	Stockholm	697765	6636572	24	1960-1983	-0.459	.024	•	•
5	A	SE110	Stockholm	697765	6636572	24	1960-1983	-0.459	.024	•	•
6	A	SE125	Västmanland	567407	6620057	9	1984-1992	•	•	0.736	.024
7	C'	SE311-A	Värmland	342159	6617789	21	1960-1980	-0.571	.007	•	•
8	A	SE311-P	Värmland	411308	6599398	24	1960-1983	-0.616	.001	•	•
9	A	SE311-P	Värmland	411308	6599398	10	1993-2002	0.733	.016	•	•
10	A	SE123	Östergötland	538284	6469121	24	1960-1983	•	•	-0.477	.018

Spearman rank correlates between red fox index and finite rate of increase $\lambda_{t \rightarrow t+1}$ in the hare populations

Abbreviations: XY - ordinates in meters (SWEREF 99) from Prime Meridian and Equator; n - sample size population indices pairs; Period – regime sequence in the red fox time series; rs - correlation coefficient; tim - correlates with mountain hares; eur - with brown hares; • - insignificant rs.

Result table on Appendix page III: Spearman rank correlation analyses between red fox and hare time series from counties in distribution region C' and A, respectively. The upper table is visualized in form of the bubble chart in Fig. 2.

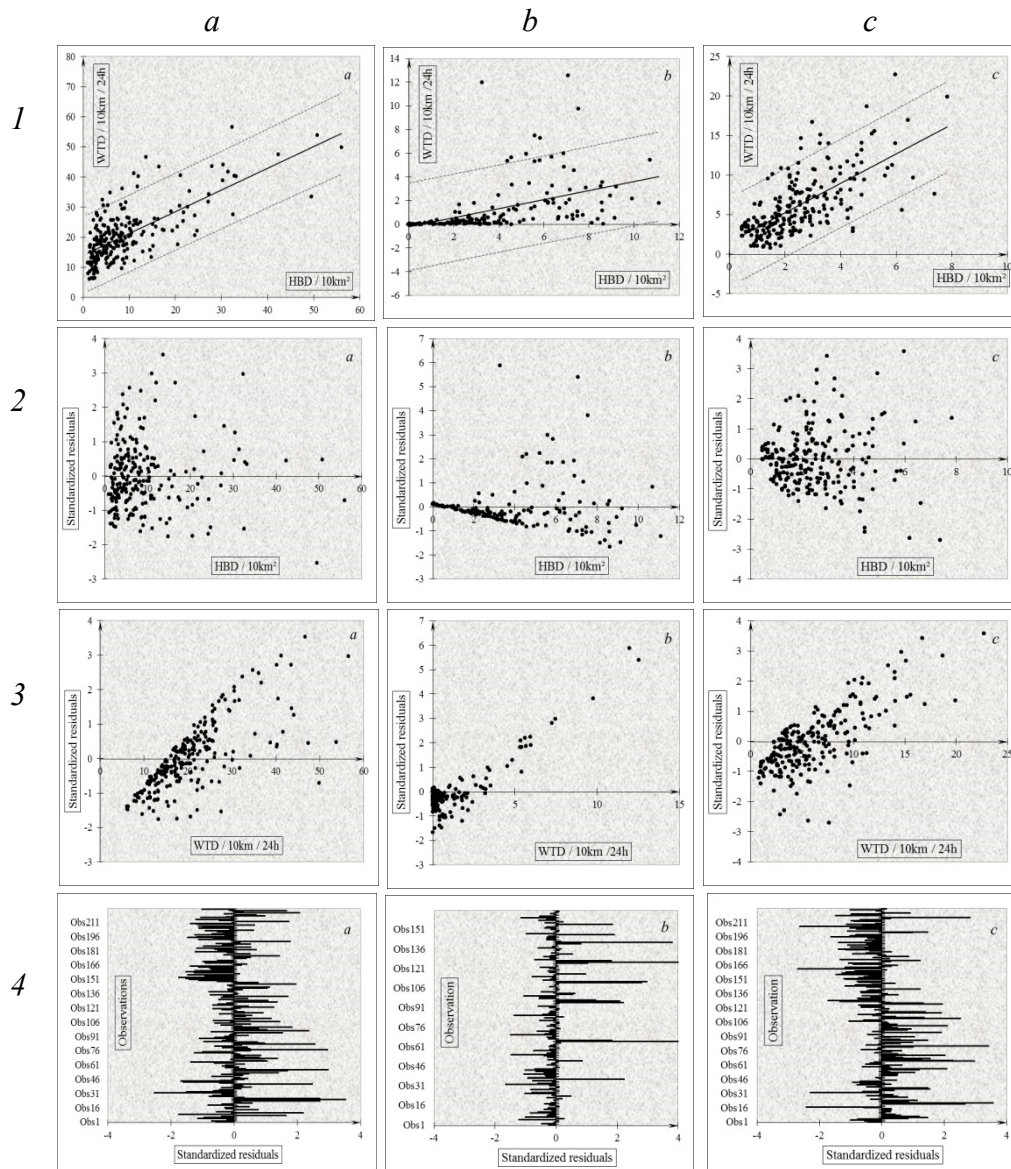
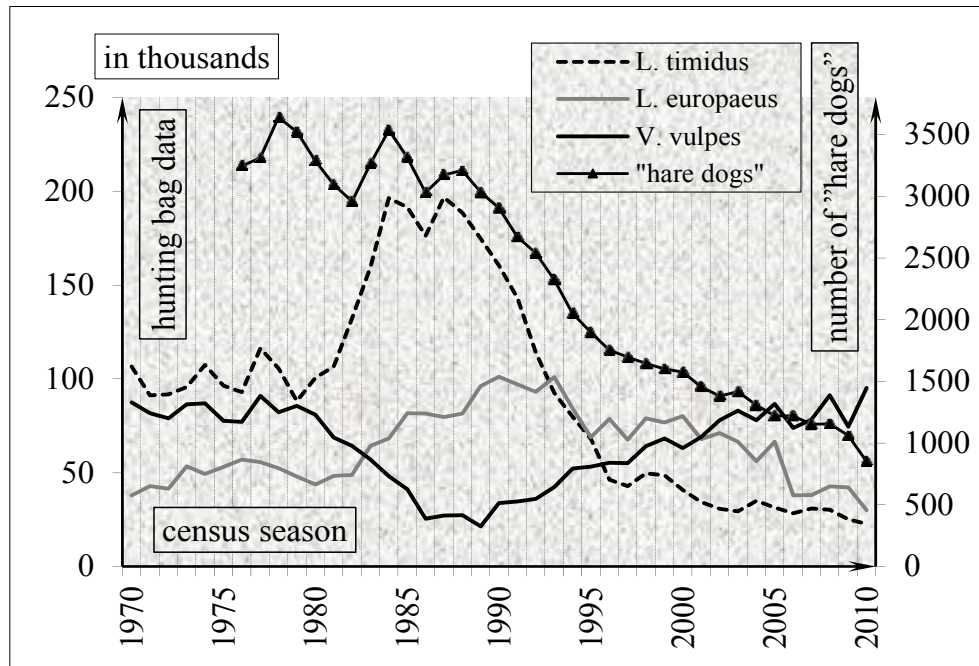
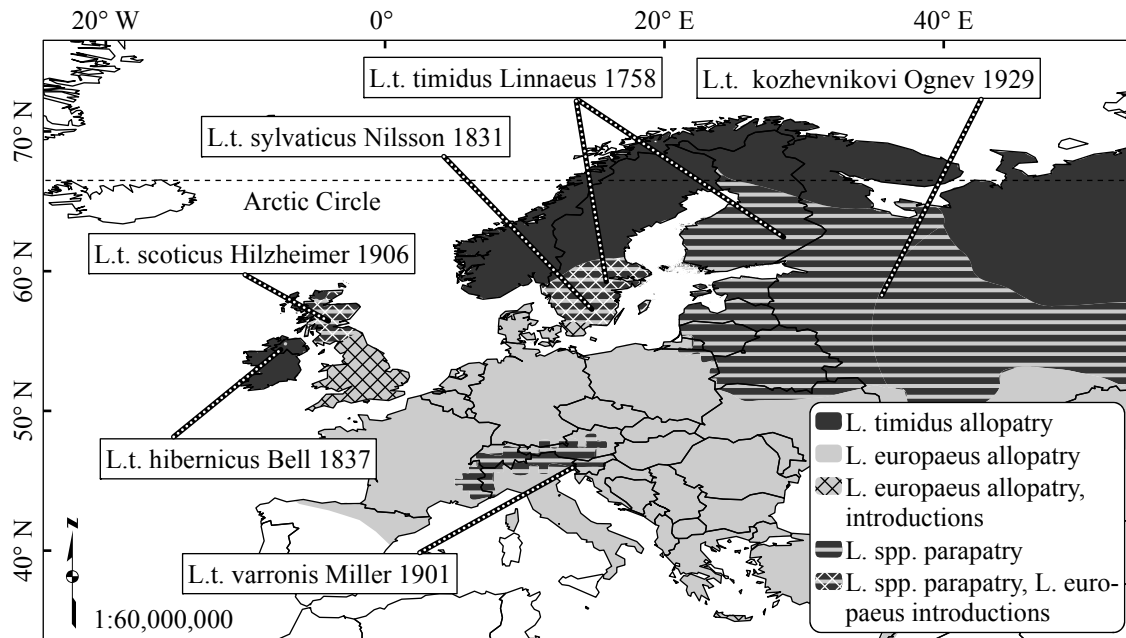


Figure output of OLS linear regression analyses of wildlife triangle data WTD on hunting bag data HBD densities from Finland through 1996 to 2010 for mountain hares (a), brown hares (b) and red foxes (c) with scatterplot, regression line and 95% CI (1), standardized residuals of HBD densities and WTD (2 and 3) and bar chart of the standardized residuals (4).



Hunting bag data time series for mountain hares, brown hares and red foxes from 1970 to 2010 on left y-axis compared to the number of pedigreed "hare dog" pups per hunting year from 1976 to 2010 on the right y-axis. The data is for Sweden and pooled at the national scale (References see text).



Biogeographic distribution of mountain hares (dark) and brown hares (light grey) in Europe and European Russia. Subspecies of mountain hares, which exist in parapatry with brown hares, are superimposed and their region of occurrence roughly pointed out (State: 1999 onwards; Geographic coordinate system: WGS 84; Graticule: Decimal degrees; References see main text).

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